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Top-down control inhibits spatial self-organization of a patterned landscape

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Abstract. Regular, self-organized spatial patterns in primary producers have been described in a wide range of ecosystems and are predicted to affect community production and resilience. Although consumers are abundant in most systems, the effect of trophic interactions on pattern formation in primary producers remains unstudied. We studied the effects of top-down control by herbivores on a self-organized landscape of regularly spaced, diatom-covered hummocks alternating with water-filled hollows on an intertidal mudflat in The Netherlands. Spatial patterns developed during spring but were followed by a rapid collapse in summer, leading to a flat landscape with low diatom densities and little variation in sediment bed level. This dramatic decline co-occurred with a gradual increase of benthic herbivores. A manipulative field experiment, where benthic herbivores were removed from the sediment, revealed that both diatom growth and hummock formation were inhibited by the activity of benthic herbivores. Our study provides clear evidence of top-down control of spatial self-organized patterns by benthic herbivores within a biological–geomorphic landscape.

Key words: biogeomorphology; diatom–sediment feedbacks; herbivory; intertidal flats; landscape formation; macrofauna; spatial self-organization; sudden regime shift; top-down control.

Introduction

Spatial self-organization has been observed in ecosystems all over the world, from tropical arid lands to boreal peat lands (Klausmeier 1999, Eppinga et al. 2009). These self-organized spatial patterns result from strong, local feedback mechanisms, whose effects can scale-up to form regular or scale-free patterns (Pascual and Guichard 2005, Rietkerk and Van de Koppel 2008). Regular patterns emerge where positive and negative feedbacks occur at different spatial scales (Rietkerk and Van de Koppel 2008). In semiarid ecosystems, for example, vegetation-induced infiltration of rain water into the sediment causes local facilitation between plants, reduces water availability at greater distances, resulting in regularly spaced vegetation patches (Klausmeier 1999, Couteron and Lejeune 2001, Von Hardenberg et al. 2001). Spatial self-organization has important implications for the functioning of ecosystems, as it can increase primary production and enhance the stability of ecological communities (Rietkerk et al. 2002, Van de Koppel and Rietkerk 2004, Van de Koppel et al. 2005).

Top-down control by herbivores on spatially patterned vegetation can have nonlinear effects on community production and resilience in self-organized systems (HilleRisLambers et al. 2001, Rietkerk et al. 2004). Despite their potential impact, little is known about the effect of top-down control on the process of self-organization within ecosystems, or about the potential for herbivores to cause catastrophic shifts in spatially self-organized vegetation (Kéfi et al. 2007). Previous model studies have predicted a breakdown of self-organization once a threshold of grazing pressure is exceeded, followed by a collapse to an homogeneous state with low vegetation cover (Rietkerk et al. 2000, HilleRisLambers et al. 2001). This collapse affects food web structure and ecosystem function because an important food source is lost. While it is well known that predator–prey interactions can cause spatial patterns in ecological communities (e.g., Huffaker 1958, Hassell et al. 1991, Maron and Harrison 1997), there is little empirical evidence for the influence of top-down control on landscape formation in a spatially self-organized ecosystem.

In this study, we test the influence of top-down control on spatial self-organization on an intertidal mudflat. In this ecosystem, a spatial pattern of elevated hummocks alternating with water-filled hollows develops each spring (Blanchard et al. 2000, de Brouwer et al. 2000, Gouleau et al. 2000, Whitehouse et al. 2000, Lanuru et al. 2007), due to a strong interaction between diatom growth and geomorphological processes (Fig. 1A; Weerman et al. 2010). Patterning on tidal flats can be a seasonal phenomenon, in particular on tidal flats where bed level differences between hummocks and hollows are small. In these systems, spatial patterns form in March–April (Fig. 1A) and disappear late May–June,

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returning to a homogenous bare landscape (Fig. 1B). Observations from this system suggest that the decline is potentially caused by increased grazing pressure by benthic animals (de Brouwer et al. 2000). The effects that macrobenthic grazers have on the interaction between diatoms and sedimentation have been investigated in a number of field and model studies (Wood and Widdows 2002, Paarlberg et al. 2005, Le Hir et al. 2007), revealing that herbivore grazing can influence sediment dynamics both directly by feeding and indirectly through bioturbation. Hence, intertidal mudflats provide a unique opportunity to investigate the effects of increasing top-down control in spatially self-organized ecosystems and to test the effects of grazing on self-organization and landscape formation in manipulative experiments.

Here, we present a study on the effect of seasonal changes in top-down control on spatial self-organization and landscape formation on an intertidal flat. We first determined seasonal changes in diatom biomass, elevation differences in the landscape, and herbivore abundance in two consecutive years. We then hypothesized that benthic herbivores cause a decline in diatom biomass and bed level differences leading to a change from a spatial self-organized landscape into a system lacking landscape patterns. To test the causality of this decline, we next performed a manipulative field experiment with defaunated sediment where we applied patches of sediment including and excluding herbivores. We hypothesize that the patches where herbivores are removed reveal increased diatom content and will maintain their bed level relative to the surrounding sediment, while the grazed plots will show a decreased diatom content and bed level. Using this combination of observational and manipulative methods, we found clear evidence for increased top-down control on spatial self-organization, changing the ecosystem from a diatom-covered, patterned mudflat into an erosive mudflat lacking spatial self-organization.

Materials and Methods

Study system

A field study was performed at the Kapellebank, a tidal flat along the edges of the Westerschelde estuary, in the Netherlands (51°27′ N; 3°58′ E). From early spring until the onset of summer, spatial diatom patterns were observed on 80% of the surface of this intertidal flat. Pattern formation is initialized when a small, random increase in sediment elevation improves diatom growth. On top of these elevations, diatoms accumulate, forming a visible brown biofilm, which in turn is strengthened by the excretion of extracellular polymeric substances (EPS) (Neumann et al. 1970). EPS inhibits erosion by increasing sediment cohesion and decreasing bottom roughness (Paterson 1989, Sutherland et al. 1998*a*, *b*). This results in an increase of sedimentation of fine-grained particles (de Brouwer et al. 2000, Montserrat et al. 2009), which subsequently stimulates diatom growth (Van de Koppel et al. 2001). In the hollows, water accumulates during low tide, inhibiting the buildup of EPS as it dissolves in the overlaying water (Blanchard et al. 2000, Paterson et al. 2000). This in turn leads to increased erosion of diatoms and sediment in the hollows during inundation. The interaction between accumulation of sediment on the hummocks and drainage of water toward the hollows generates a scale-dependent feedback of small-scale facilitation and larger-scale inhibition of diatom growth. This scale-dependent feedback provides a possible explanation for spatial pattern formation when herbivore densities are low (Weerman et al. 2010). In the Westerschelde estuary, a peak in microphytobenthos occurs in April–June (Herman et al. 2001, Montserrat et al. 2008). During this period, spatial patterns are clearly present at several locations in the estuary, but disappear from the end of May onward, not returning until spring next year (de Brouwer et al. 2000).

Field observations

To investigate whether increased herbivore numbers are coincident with observed collapse of self-organized diatom patterns and the co-occurring physical landscape on intertidal flats, we monitored macrobenthic animal densities from February until the patterns had disappeared in June in both 2007 and 2008. In 1–2 week intervals during each year, we sampled diatom biomass, macrofauna density, sediment grain size profiles, and elevation differences between hummocks and hollows. Sediment depth profiles were determined monthly April–June in 2007. In 2008, the temporal sampling frequency was lower compared to 2007, as the sampling in 2008 was done to determine consistency of the pattern found in 2007 for patchiness of diatoms and influence of macrofauna.

Difference in relative bed level elevation between hummocks and their adjacent hollows, was measured using a plastic white grid board (0.85 × 0.50 m). The board was pushed in and placed level to the sediment, set perpendicular to the patches in such a way that the grid board included the lowest and highest point of a hollow and hummock, respectively. A digital photo (2560 × 1920 pixels) was taken of the white grid board, and the photographs were geo-referenced and geo-corrected using Erdas image processing software (Erdas Imagine Professional version 9.3; Erdas, Atlanta, Georgia, USA). To distinguish between the grid board and sediment, an unsupervised classification was made using the image processing software. After classification the topographic profiles were extracted and a value of relative bed level height of every 0.25 cm along the board was calculated (for the detailed procedure of these methods see van der Wal et al. 2005). Bed level differences at each location were determined from this image as the difference between maximum and minimum bed level over the entire horizontal range.

To measure diatom biomass on the intertidal flat, chlorophyll *a* content in the top layer of the sediment was determined as a measure for diatom biomass on

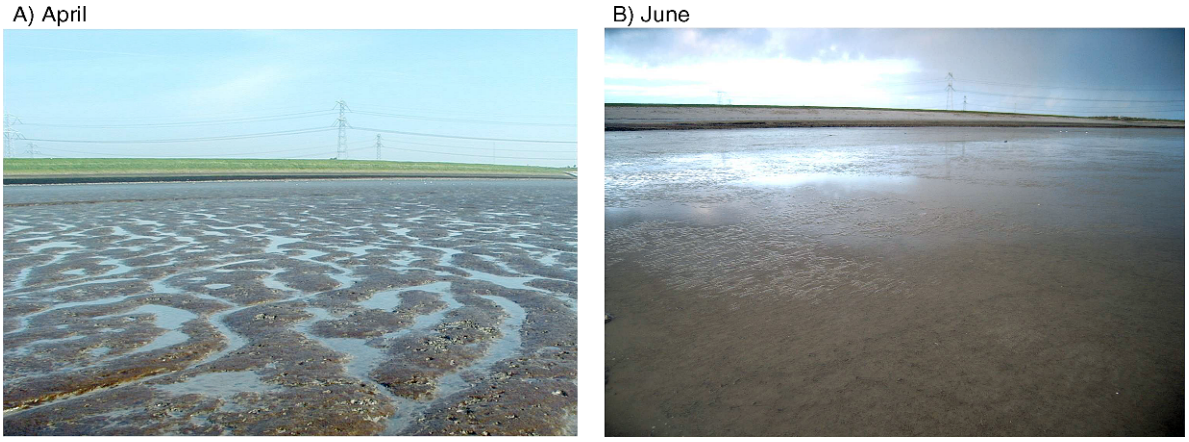

FIG. 1. Photographs of the intertidal flat at the Kapellebank, The Netherlands. (A) In April, a spatially patterned intertidal flat with hummocks and hollows is visible. (B) These patterns have disappeared in June, and the landscape has changed into a homogenous intertidal flat with low diatom biomass. Photo credit: J. Van de Koppel.

hummocks. Samples were taken of the upper 2 mm of the sediment with a 100-mL syringe, where the end was cut off (inner diameter [ID] 36 mm). Samples ($n = 5$) were placed on ice during fieldwork and stored at −80°C upon arrival in the laboratory. Pigment extraction was done by adding 10 mL 90% acetone to lyophilized sediment followed by chlorophyll *a* quantification by high-pressure liquid chromatography (HPLC) of the supernatant (Jeffrey and Humphrey 1975). Chlorophyll *a* concentrations are expressed as μg chlorophyll *a* per gram dry sediment (μg/g).

Macrofauna density was measured adjacent to the sediment samples taken to determine diatom content. Twenty centimeter deep macrofauna samples ($n = 3$ samples) were extracted using a core (ID 11 cm). The cores were sieved through a 0.5-mm mesh size and fixed with a neutralized 8% formalin solution. Prior to analysis, samples were colored using 0.01% Rose Bengal. The identification of macrofauna in the cores was done up to genus level to determine the most abundant taxa and calculate total macrofauna abundance.

We monitored changes in sediment grain size along depth profiles, as changes in grain size distribution could reflect accumulation of fine-grained sediment during pattern formation. Samples for sediment grain size analysis ($n = 5$) were taken using a syringe, with the end cut off (ID 36 mm), at the beginning of April, May, and June in 2007. Samples were kept on ice during the fieldwork before they were sliced at depths of 0–0.5, 0.5–1.0, 1.0–1.5, 1.5–2.0, 2.0–3.5, and 3.5–5 cm in the laboratory. These subsamples were freeze-dried, after which the silt and clay content was determined as the fraction of the sediment that is smaller than 63 μm using a particle size analyzer (Malvern Mastersizer 2000,Worcestershire, UK). This fraction included both clay (<2 μm) and silt particles (2–63 μm); therefore we refer to this fraction as mud content in the rest of the paper.

Testing the effects of benthic herbivores

A manipulative field experiment was carried out to test the influence of benthic herbivores on the disappearance of spatial patterns. We compared differences in diatom growth and sediment elevation change between natural sediment and sediment where herbivores were removed. The experiment was carried out in May 2007 when diatom patterns had disappeared. Prior to the experiment, sediment obtained from the intertidal flat was frozen (−20°C) for 48 h, removing all living macrofauna from the sediment. After defrosting, the sediment was taken back to the intertidal flat where it was applied on the ambient sediment surface. Either natural or defaunated sediment was applied in a round cut-off tube (ID 32 cm), where 4 L of sediment was added (Fig. 2A), resulting in hummocks that were slightly smaller compared to the natural hummocks. The cut-off tube was removed after application, which resulted in a patch of sediment with macrofauna and without macrofauna (Fig. 2B). The defaunated sediment was applied on a plastic sheet to prevent animals from below to enter, taking care that this sheet was not exposed. Each treatment was replicated five times. Sediment bed level and chlorophyll *a* content were measured as described previously, at the start of the experiment and after nine days. The sediment bed level difference between the top of the hummock with the surrounding sediment was taken as measure for hummock bed level. Hummock formation was calculated as the difference in hummock bed level at the start and end of the experiment. Similarly the difference between chlorophyll *a* concentration at the start and end of the experiment was taken as measure for relative changes in diatom content. We tested the effectiveness of our treatment by sampling macrofauna density at the end of the experiment.

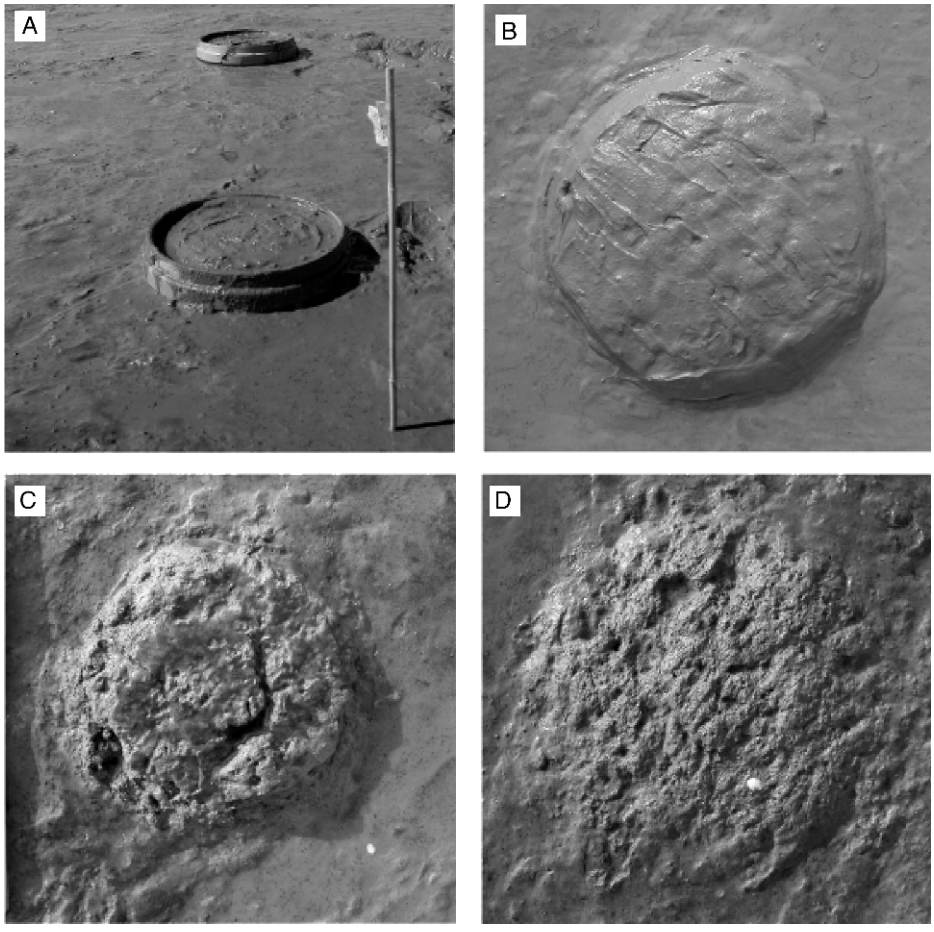

FIG. 2. We studied the effects of top-down control by herbivores on a self-organized landscape of regularly spaced, diatom-covered hummocks alternating with water-filled hollows on an intertidal mudflat. Photographs show (A) the experimental setup of the manipulative field measurement with tubes filled with 4 L of sediment, (B) artificial hummock after removal of the tube, (C) patches after nine days of experiments where herbivores were removed, and (D) patches after nine days of experiments where herbivores were present. The area photographed in panels (B), (C), and (D) is 50 × 50 cm. Photo credit: E. Weerman.

Statistical analysis

One-way ANOVA was used to identify changes in diatom content, macrofauna density, and patchiness for the separate sampling dates for both years of the observational study, followed by Tukey's hsd post hoc comparison. Normal distribution of the data was ensured by visual inspection of Q–Q plots, and Levene's test was used to check for homogeneity of variances. In cases where the data were not normally distributed, log-transformation was performed. An ANOVA was performed with sampling date and vertical distribution as treatments to identify a possible interactive effect of vertical distribution and month on mud content. The experimental data were analyzed using Welch's two-sample *t* test (one-tailed). All statistics were computed using R (*available online*).[4]

[4] ⟨http://www.R-project.org⟩

RESULTS

During both years, we observed a gradual increase in benthic diatom biomass early in the season, until chlorophyll *a* concentrations in the upper 2 mm reached values of 150–180 μg/g. Then, within about a month, chlorophyll *a* concentrations dropped to levels below 50 μg/g (Fig. 3A, B; $P < 0.001$). This decrease was particularly strong in 2007 and appeared to be more gradual in 2008. Bed level differences also decreased significantly during this period, although the decrease was more gradual (Fig. 3C, D; $P < 0.001$). During the season, this process seemed to be irreversible. Once the diatom mats had disappeared, bed level variation decreased and did not come back during the remainder of the year (de Brouwer et al. 2000). Macrofaunal densities did increase slightly during the period of diatom disappearance in both 2007 and 2008 (Appendix). After the rapid disappearance of benthic diatoms, bed level differences declined, and macrofauna, mostly animals that feed on benthic diatoms and bioturbate the

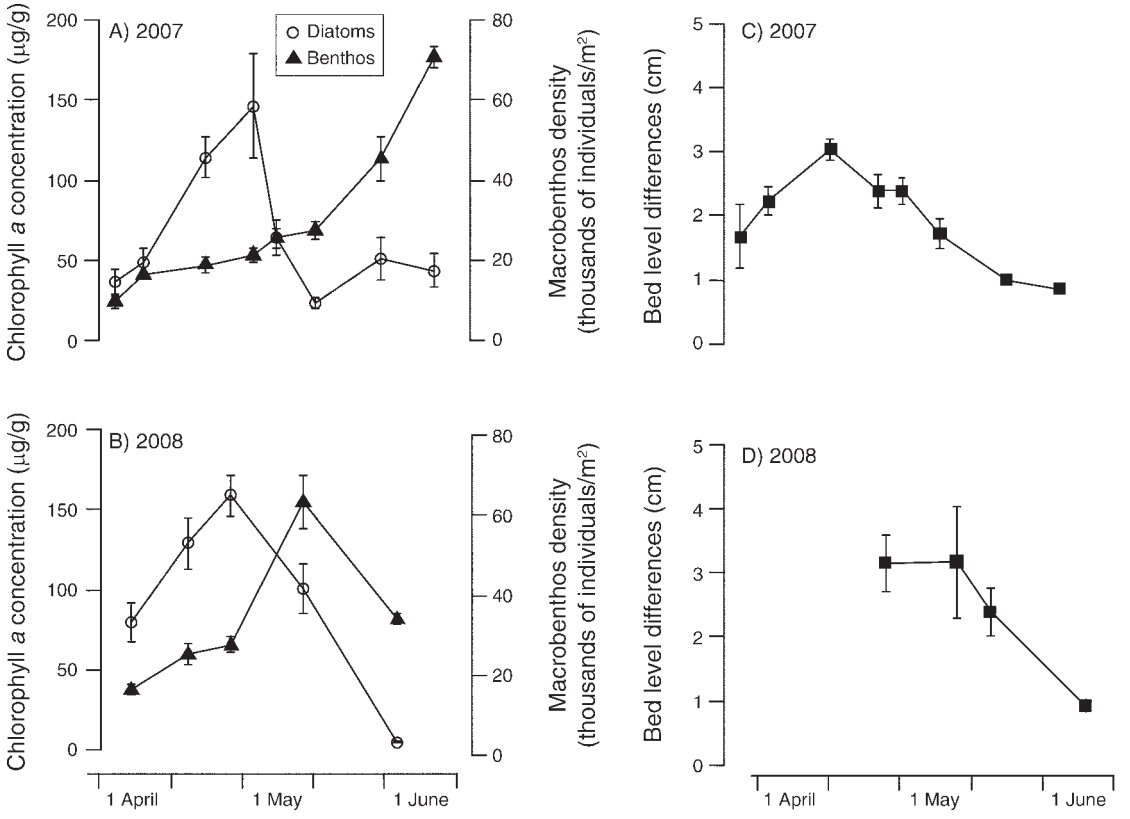

FIG. 3. Density (mean ± SE) of diatoms, as reflected by chlorophyll *a* concentration (open circles, $n = 5$ samples on hummocks), and macrobenthos (solid triangles, $n = 3$ samples on hummocks) and bed level differences between hummocks and hollows (solid squares, $n = 5$ samples) for each date shown for 2007 and 2008. Chlorophyll *a* content is a proxy for diatom biomass. Bed level differences are the differences between the sediment bed level of the hummock compared to the adjacent hollow.

sediment like *Aphelochaeta*, *Corophium*, and *Macoma*, increased very rapidly (Appendix). These bioturbating taxa dominated >80% of the total benthic herbivore abundances we found, while a minor fraction (<5%) were omnivores. Moreover, mud content in the sediment was reduced and homogenized in depth when macrofauna became more abundant (Fig. 4). Analysis of mud content revealed that month explained a significant part of the variance ($P < 0.001$), indicating that the mud content was significantly higher in April compared to May and June. There was also a vertical distribution in mud content where the mud content was significantly higher in the top layer (0–1 cm) in April and May (Fig. 4; $P < 0.001$), while in June the mud content in the top layer was equal to lower layers (Fig. 4; $P > 0.05$).

Experimental test of herbivore influence

The manipulative experiment carried out to test the effect of herbivores on pattern formation and diatom biomass revealed a striking effect of herbivory on both hummock formation and diatom growth. Diatom biomass was significantly higher in defaunated sediments (Fig. 5A; $P < 0.05$), being an order of magnitude greater compared to untreated sediment. In addition, nine days after herbivore removal, hummock bed level

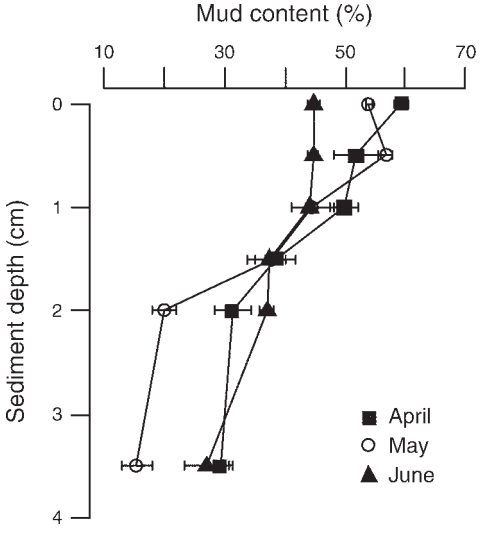

FIG. 4. Percentage mud (mean ± SE; sum of the silt and clay fractions; i.e., percentage of the sediment with particle size <63 μm) at different sediment depths at the beginning of April, May, and June 2007.

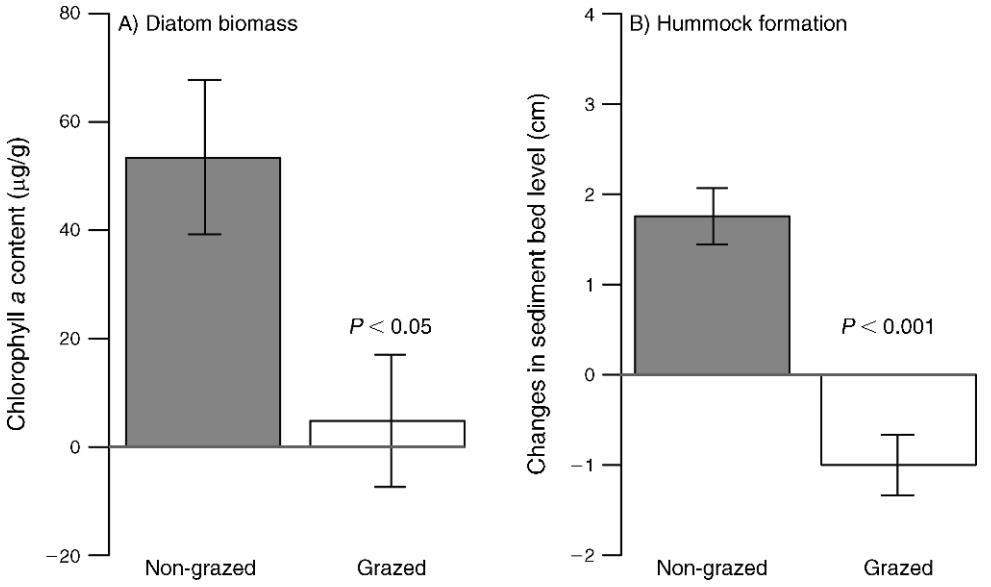

FIG. 5. Relative differences in (A) chlorophyll *a* concentration and (B) bed level (all values mean ± SE) of the field experiment with two treatments: non-grazed (gray bars, $n = 5$) and grazed (white bars, $n = 5$).

increased by nearly 2 cm in the defaunated treatments, most likely due to the combined effects of sedimentation within the experimental patches and erosion around the patches. In contrast, hummock bed level decreased in the treatment where herbivores were present (Fig. 5B; $P < 0.001$), resulting from erosion on top of the patches. Nine days after treatment application, macrofauna densities were 10 times lower in the defaunated treatments ($2.8 \pm 0.7 \times 1000$ individuals/m^2, mean ± SE) compared to the controls ($24.3 \pm 6.3 \times 1000$ individuals/m^2), showing that the effect of our treatment lasted for the entire experimental period.

DISCUSSION

Our results reveal a clear top-down effect of herbivores causing the disappearance of self-organized spatial patterns of diatoms and the co-occurring physical landscape. In each of the two consecutive years, a gradual buildup of diatom biomass in the top layer of the sediment was followed by a rapid decline of benthic diatoms to very low biomass, co-occurring with a gradual buildup of benthic animal numbers. During this transition, the landscape changed from a regular pattern of hummocks and hollows into a flat homogeneous landscape with no visible diatom biofilms. The onset of the diatom population collapse begins after several macrobenthos species, particular *Macoma* larvae, have settled on the intertidal flat, which was particularly evident in 2007. Benthic invertebrates predominantly prefer primary settlement at sites with high diatom biomass and EPS content (Keough and Raimondi 1995, Dahms et al. 2004, Patil and Anil 2005, Jouuchi et al. 2007, Van Colen et al. 2009). Thus the importance of benthic diatoms and associated EPS content on top of the hummocks for settlement of larvae from the water column is evident. A manipulative field experiment revealed that benthic herbivores prevent diatoms from stabilizing the sediment, and thereby may block the mechanism of spatial self-organization, as the absence of herbivores resulted in the reoccurrence of hummocks on the intertidal flat. Our study highlights that the effect of top-down control can extend beyond the direct effect of consumption of the prey community in self-organized ecosystems.

Our results are in close agreement with the predictions of theoretical studies on self-organized patterns generated in other systems including arid ecosystems. Mathematical models have predicted that, along a gradient of herbivore impact, arid vegetation undergoes a transition from self-organized spatial patterns to a homogeneous degraded state without vegetation (HilleRisLambers et al. 2001). Increasing density of benthic herbivores, possibly co-occurring with physical disturbance (e.g., wind-induced waves), disabled the formation of self-organized patterns on intertidal flats. This resulted in a collapse of the spatially patterned system that was seen in both years of observation. Although the general predictions are consistent with observational studies on the effects of increased grazing on patch formation in arid grasslands (Rietkerk et al. 2000, Nash et al. 2003, Stavi et al. 2009), experimental evidence for the effects of grazing on the formation of spatial vegetation patterns, and on the interaction between plants and abiotic processes, is limited. Our experimental results confirm the hypothesis that grazing affects the functioning (e.g., sediment accretion and diatom biomass) of self-organized landscapes by interfering with feedbacks between organisms and sedimentary process-

es. Mechanisms resulting in spatial patterns that act on intertidal flats and semiarid ecosystems are different and the temporal scale of the effect is much shorter on intertidal flats compared to arid ecosystems. Hence, increased top-down control appears to have similar effects in both ecosystems, emphasizing the generality of our results.

The importance of predator–prey relations and top-down control for spatial self-organization has mostly been studied in systems where predator–prey interactions are the cause of spatial patterns (Huffaker 1958, Hassell et al. 1991). The occurrence of spatial patterns in predator–prey systems are, for example, observed in insect parasitoid–host interactions (Maron and Harrison 1997). In our system, the benthic grazers are important, yet they are not part of the process that causes spatial pattern formation. These grazers rather form a higher trophic level that influences pattern formation by reducing the density of one of the components of the pattern-forming feedback, the diatoms. Herbivores reduce diatom biomass and associated EPS (de Deckere et al. 2001); this can cause a failure of the diatom–sedimentation feedback. Herbivores may block the spatial self-organization as a landscape-forming process and in the end induce a flat degraded landscape that lacks significant diatom cover. Prior research has shown that benthic herbivores themselves are under top-down control by predators, e.g., migratory birds (Daborn et al. 1993), emphasizing the importance of top-down control in influencing the spatial structure and functioning of intertidal ecosystems.

It is likely that in our system, the decline of diatom biomass cannot be solely explained by direct grazing, but is partly due to the indirect effects of benthic herbivores due to bioturbation and its physical effect on diatom biofilm integrity. Most species we found (>80%) are deposit feeders, which feed from a funnel and crawl through or over the sediment while feeding on the diatoms (Ysebaert et al. 2003). While feeding, these herbivores mix sediment and the attached benthic algae (Solan et al. 2003), and may inhibit the buildup of mud in the upper layers of the sediment (Mermillod-Blondin et al. 2004). These indirect effects of benthic grazing in part explain the dramatic decline in benthic algae. Moreover, a number of studies emphasize that, in general, only a small fraction of benthic primary production on tidal flats is directly grazed by macrobenthos (Herman et al. 2000, Van Colen et al. 2010). Nevertheless, the taxa we find just before and during the collapse, e.g., *Corophium*, *Macoma*, and *Aphelochaeta*, feed mostly on benthic diatoms, as is evidenced by their stable isotope ratio (Herman et al. 2000). Hence, their biomass is mostly supported by local diatom primary production, which implies that the intensity of bioturbation is an indirect effect of grazing. Similar effects of herbivore bioturbation affecting sediment texture and soil erosion have been observed on intertidal flats (e.g., Widdows et al. 2000), salt marshes (e.g., van Wesenbeeck et al. 2007), and in terrestrial ecosystems (e.g., Stavi et al. 2009). For example in arid ecosystems trampling by herbivores results in water loss and erosion (Stavi et al. 2009). In arctic tundra ecosystems, grubbing of vegetation by geese has a devastating effect on plants, changing large areas of marsh to bare mud (Jefferies 1988, Iacobelli and Jefferies 1991). This shows that both in terrestrial as well as estuarine ecosystems, herbivores can impose strong indirect effects on biotic components of the ecosystem as a consequence of their grazing, thereby changing landscape morphology.

Ecosystems that exhibit strong feedback mechanisms are associated with catastrophic shifts and bistability, where sudden, irreversible switches to alternative states may occur in response to gradually changing environmental conditions (Scheffer et al. 2001). Spatial patterns can indicate the presence of, and proximity to, a switch point (Rietkerk et al. 2004, Kéfi et al. 2007). The co-occurrence of both self-organized spatial patterns and a dramatic decline of diatom biomass during spring, in particular in 2007, suggest that two stable states may occur on intertidal flats (Van de Koppel et al. 2001). However, a field experiment where diatom patterns and landscape structure were removed using floor sweepers, showed complete recovery of both diatoms and hummocks within two weeks, indicating the absence of alternative stable states (Weerman et al. 2010). Although this experiment was replicated three times during the season until just before the transition into the flat sediment state, no differences between treatments in recovery time were found (Weerman et al. 2010). Hence, we have no conclusive evidence for considering them as a catastrophic shift between alternate stable states, even though the decline of diatom biomass was dramatic. Nevertheless, the collapse of diatom densities was striking and remarkably occurs at a density of ~20 000 individuals/m^2 in both years. This could indicate that there is a macrobenthos density threshold at which the collapse occurs. The precise position of this threshold is likely to vary from system to system, as sedimentary characteristics (e.g., water content) and physical forcing (e.g., winds) also play a role in determining the erodability of sediments (de Brouwer et al. 2000, Tolhurst et al. 2008). Diatom biomass can decrease rapidly when exposed to offshore winds, even at relatively low wind speeds (de Jonge and van Beusekom 1995, de Brouwer et al. 2000). In 2007, stronger winds were present when diatoms were declining, while conditions in 2008 were less severe, providing a possible explanation for the stronger collapse in 2007 relative to 2008 (Dutch Ministry of Transport, Public Works, and Water Management; data *available online*).[5] Hence, it is possible that multiple factors are responsible for the dramatic decline that is observed in 2007. Nevertheless

[5] ⟨http://www.hmcz.nl⟩

our experiment clearly identifies top-down control as an important factor in determining diatom densities.

Our study highlights that the effect of top-down control can extend beyond the direct effect of consumption of the prey community in self-organized ecosystems. By lowering diatom stocks, benthic herbivores inhibit the diatom–sediment feedback, which is responsible for the spatial self-organization, resulting in the disappearance of self-organized spatial patterns of diatoms and the co-occurring physical landscape. Loss of self-organization has far-reaching implications for intertidal ecosystems. During this diatom collapse, the sediment bed level becomes more erosive and as a consequence the sediment stored in the hummocks is lost to the overlying water within a few weeks. This loss can affect the entire benthic community (Montserrat et al. 2008), as sediment is an important source of nutrients (Van de Koppel et al. 2001) and organic matter (Herman et al. 2000). Moreover, the eroded sediment can increase water turbidity and can thereby affect planktonic as well as benthic primary production (Herman et al. 2001, Staats et al. 2001). Hence, by disabling self-organization processes, top-down control can dramatically influence both community structure and ecosystem functioning.

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Literature Cited

Blanchard, G. F., D. M. Paterson, L. J. Stal, P. Richard, R. Galois, V. Huet, J. Kelly, C. Honeywill, J. de Brouwer, K. Dyer, M. Christie, and M. Seguignes. 2000. The effect of geomorphological structures on potential biostabilisation by microphytobenthos on intertidal mudflats. Continental Shelf Research 20:1243–1256.

Couteron, P., and O. Lejeune. 2001. Periodic spotted patterns in semi-arid vegetation explained by a propagation-inhibition model. Journal of Ecology 89:616–628.

Daborn, G. R., C. L. Amos, M. Brylinsky, H. Christian, G. Drapeau, R. W. Faas, J. Grant, B. Long, D. M. Paterson, G. M. E. Perillo, and M. C. Piccolo. 1993. An ecological cascade effect: migratory birds affect stability of intertidal sediments. Limnology and Oceanography 38:225–231.

Dahms, H. U., S. Dobretsov, and P. Y. Qian. 2004. The effect of bacterial and diatom biofilms on the settlement of the bryozoan *Bugula neritina*. Journal of Experimental and Marine Biology and Ecology 313:191–209.

de Brouwer, J. F. C., S. Bjelic, E. de Deckere, and L. J. Stal. 2000. Interplay between biology and sedimentology in a mudflat (Biezelingse Ham, Westerschelde, The Netherlands). Continental Shelf Research 20:1159–1177.

de Deckere, E., T. J. Tolhurst, and J. F. C. de Brouwer. 2001. Destabilization of cohesive intertidal sediments by infauna. Estuarine Coastal and Shelf Science 53:665–669.

de Jonge, V. N., and J. E. E. van Beusekom. 1995. Wind-induced and tide-induced resuspension of sediment and microphytobenthos from tidal flats in the Ems Estuary. Limnology and Oceanography 40:766–778.

Eppinga, M. B., P. C. de Ruiter, M. J. Wassen, and M. Rietkerk. 2009. Nutrients and hydrology indicate the driving mechanisms of peatland surface patterning. American Naturalist 173:803–818.

Gouleau, D., J. M. Jouanneau, O. Weber, and P. G. Sauriau. 2000. Short- and long-term sedimentation on Montportail-Brouage intertidal mudflat, Marennes-Oleron Bay (France). Continental Shelf Research 20:1513–1530.

Hassell, M. P., H. N. Comins, and R. M. May. 1991. Spatial structure and chaos in insect population dynamics. Nature 353:255–258.

Herman, P. M. J., J. J. Middelburg, and C. H. R. Heip. 2001. Benthic community structure and sediment processes on an intertidal flat: results from the ECOFLAT project. Continental Shelf Research 21:2055–2071.

Herman, P. M. J., J. J. Middelburg, J. Widdows, C. H. Lucas, and C. H. R. Heip. 2000. Stable isotopes as trophic tracers: combining field sampling and manipulative labelling of food resources for macrobenthos. Marine Ecology Progress Series 204:79–92.

HilleRisLambers, R., M. Rietkerk, F. van den Bosch, H. H. T. Prins, and H. de Kroon. 2001. Vegetation pattern formation in semi-arid grazing systems. Ecology 82:50–61.

Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator–prey oscillations. Hilgardia 27:343–383.

Iacobelli, A., and R. L. Jefferies. 1991. Inverse salinity gradients in coastal marshes and the death of stands of *Salix*: the effects of grubbing by geese. Journal of Ecology 79:61–73.

Jefferies, R. L. 1988. Vegetational mosaics: plant–animal interactions, and resources for plant growth. Chapman and Hall, London, UK.

Jeffrey, S. W., and G. F. Humphrey. 1975. New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. Biochemie und Physiologie der Pflanzen 167:191–194.

Jouuchi, T., C. G. Satuito, and H. Kitamura. 2007. Sugar compound products of the periphytic diatom *Navicula ramosissima* induce larval settlement in the barnacle, *Amphibalanus amphitrite*. Marine Biology 152:1065–1076.

Kéfi, S., M. Rietkerk, C. L. Alados, Y. Pueyo, V. P. Papanastasis, A. ElAich, and P. C. de Ruiter. 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. Nature 449:213–217.

Keough, M. J., and P. T. Raimondi. 1995. Responses of settling invertebrate larvae to bioorganic films: effects of different types of films. Journal of Experimental Marine Biology and Ecology 185:235–253.

Klausmeier, C. A. 1999. Regular and irregular patterns in semiarid vegetation. Science 284:1826–1828.

Lanuru, M., R. Riethmuller, C. van Bernem, and K. Heymann. 2007. The effect of bedforms (crest and trough systems) on sediment erodibility on a back-barrier tidal flat of the East Frisian Wadden Sea, Germany. Estuarine Coastal and Shelf Science 72:603–614.

Le Hir, P., Y. Monbet, and F. Orvain. 2007. Sediment erodability in sediment transport modelling: Can we account for biota effects? Continental Shelf Research 27:1116–1142.

Maron, J. L., and S. Harrison. 1997. Spatial pattern formation in an insect host–parasitoid system. Science 278:1619–1621.

Mermillod-Blondin, F., R. Rosenberg, F. Francois-Carcaillet, K. Norling, and L. Mauclaire. 2004. Influence of bioturbation by three benthic infaunal species on microbial communities and biogeochemical processes in marine sediment. Aquatic Microbial Ecology 36:271–284.

Montserrat, F., C. Van Colen, S. Degraer, T. Ysebaert, and P. M. J. Herman. 2008. Benthic community-mediated sediment dynamics. Marine Ecology Progress Series 372: 43–59.

Montserrat, F., C. Van Colen, P. Provoost, M. Milla, M. Ponti, K. Van den Meersche, T. Ysebaert, and P. M. J. Herman. 2009. Sediment segregation by biodiffusing bivalves. Estuarine Coastal and Shelf Science 83:379–391.

Nash, M. S., E. Jackson, and W. G. Whitford. 2003. Soil microtopography on grazing gradients in Chihuahuan desert grasslands. Journal of Arid Environments 55:181–192.

Neumann, A. C., C. D. Gebelein, and T. P. Scoffin. 1970. Composition, structure and erodability of subtidal mats, Abaco, Bahamas. Journal of Sedimentary Petrology 40:274–297.

Paarlberg, A. J., M. A. F. Knaapen, M. B. de Vries, S. Huscher, and Z. B. Wang. 2005. Biological influences on morphology and bed composition of an intertidal flat. Estuarine Coastal and Shelf Science 64:577–590.

Pascual, M., and F. Guichard. 2005. Criticality and disturbance in spatial ecological systems. Trends in Ecology and Evolution 20:88–95.

Paterson, D. M. 1989. Short-term changes in the erodibility of intertidal cohesive sediments related to the migratory behavior of epipelic diatoms. Limnology and Oceanography 34:223–234.

Paterson, D. M., T. J. Tolhurst, J. A. Kelly, C. Honeywill, E. de Deckere, V. Huet, S. A. Shayler, K. S. Black, J. de Brouwer, and I. Davidson. 2000. Variations in sediment properties, Skeffling mudflat, Humber Estuary, UK. Continental Shelf Research 20:1373–1396.

Patil, J. S., and A. C. Anil. 2005. Influence of diatom exopolymers and biofilms on metamorphosis in the barnacle *Balanus amphitrite*. Marine Ecology Progress Series 301:231–245.

Rietkerk, M., M. C. Boerlijst, F. van Langevelde, R. HilleRisLambers, J. Van de Koppel, L. Kumar, H. H. T. Prins, and A. M. de Roos. 2002. Self-organization of vegetation in arid ecosystems. American Naturalist 160:524–530.

Rietkerk, M., S. C. Dekker, P. C. de Ruiter, and J. Van de Koppel. 2004. Self-organized patchiness and catastrophic shifts in ecosystems. Science 305:1926–1929.

Rietkerk, M., P. Ketner, J. Burger, B. Hoorens, and H. Olff. 2000. Multiscale soil and vegetation patchiness along a gradient of herbivore impact in a semi-arid grazing system in West Africa. Plant Ecology 148:207–224.

Rietkerk, M., and J. Van de Koppel. 2008. Regular pattern formation in real ecosystems. Trends in Ecology and Evolution 23:169–175.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature 413: 591–596.

Solan, M., et al. 2003. Towards a greater understanding of pattern, scale and process in marine benthic systems: a picture is worth a thousand worms. Journal of Experimental and Marine Biology and Ecology 285:313–338.

Staats, N., E. de Deckere, B. de Winder, and L. J. Stal. 2001. Spatial patterns of benthic diatoms, carbohydrates and mud on a tidal flat in the Ems-Dollard estuary. Hydrobiologia 448:107–115.

Stavi, I., H. Lavee, E. D. Ungar, and P. Sarah. 2009. Ecogeomorphic feedbacks in semiarid rangelands: a review. Pedosphere 19:217–229.

Sutherland, T. F., C. L. Amos, and J. Grant. 1998*a*. The effect of buoyant biofilms on the erodibility of sublittoral sediments of a temperate microtidal estuary. Limnology and Oceanography 43:225–235.

Sutherland, T. F., J. Grant, and C. L. Amos. 1998*b*. The effect of carbohydrate production by the diatom *Nitzschia curvilineata* on the erodibility of sediment. Limnology and Oceanography 43:65–72.

Tolhurst, T. J., M. Consalvey, and D. M. Paterson. 2008. Changes in cohesive sediment properties associated with the growth of a diatom biofilm. Hydrobiologia 596:225–239.

Van Colen, C., J. Lenoir, A. De Backer, B. Vanelslander, M. Vincx, S. Degraer, and T. Ysebaert. 2009. Settlement of *Macoma balthica* larvae in response to benthic diatom films. Marine Biology 156:2161–2171.

Van Colen, C., F. Montserrat, M. Vincx, P. M. J. Herman, T. Ysebaert, and S. Degraer. 2010. Macrobenthos recruitment success in a tidal flat: feeding trait dependent effects of disturbance history. Journal of Experimental and Marine Biology 385:79–84.

Van de Koppel, J., P. M. J. Herman, P. Thoolen, and C. H. R. Heip. 2001. Do alternate stable states occur in natural ecosystems? Evidence from a tidal flat. Ecology 82:3449–3461.

Van de Koppel, J., and M. Rietkerk. 2004. Spatial interactions and resilience in arid ecosystems. American Naturalist 163: 113–121.

Van de Koppel, J., M. Rietkerk, N. Dankers, and P. M. J. Herman. 2005. Scale-dependent feedback and regular spatial patterns in young mussel beds. American Naturalist 165: E66–E77.

van der Wal, D., P. M. J. Herman, and A. Wielemaker-van den Dool. 2005. Characterisation of surface roughness and sediment texture of intertidal flats using ERS SAR imagery. Remote Sensing of Environment 98:96–109.

van Wesenbeeck, B. K., J. Van de Koppel, P. M. J. Herman, J. P. Bakker, and T. J. Bouma. 2007. Biomechanical warfare in ecology; negative interactions between species by habitat modification. Oikos 116:742–750.

Von Hardenberg, J., E. Meron, M. Shachak, and Y. Zarmi. 2001. Diversity of vegetation patterns and desertification. Physical Review Letters 8719.

Weerman, E. J., J. Van de Koppel, M. B. Eppinga, F. Montserrat, Q. X. Liu, and P. M. J. Herman. 2010. Spatial self-organization on intertidal mudflats through biophysical stress divergence. American Naturalist 176:E15–E32.

Whitehouse, R. J. S., P. Bassoullet, K. R. Dyer, H. J. Mitchener, and W. Roberts. 2000. The influence of bedforms on flow and sediment transport over intertidal mudflats. Continental Shelf Research 20:1099–1124.

Widdows, J., M. D. Brinsley, P. N. Salkeld, and C. H. Lucas. 2000. Influence of biota on spatial and temporal variation in sediment erodability and material flux on a tidal flat (Westerschelde, The Netherlands). Marine Ecology Progress Series 194:23–37.

Wood, R., and J. Widdows. 2002. A model of sediment transport over an intertidal transect, comparing the influences of biological and physical factors. Limnology and Oceanography 47:848–855.

Ysebaert, T., P. M. J. Herman, P. Meire, J. Craeymeersch, H. Verbeek, and C. H. R. Heip. 2003. Large-scale spatial patterns in estuaries: estuarine macrobenthic communities in the Schelde estuary, NW Europe. Estuarine Coastal and Shelf Science 57:335–355.

APPENDIX

Cumulative abundances of the most abundant macrofauna taxa in 2007 and 2008 (*Ecological Archives* E092-042-A1).